Nature Conservation

Nature Conservation 58: 1–10 (2025)
DOI: 10.3897/natureconservation.58.129016

Research Article

On the path to extinction: *Helix godetiana* Kobelt, 1878, the only threatened *Helix* species in Greece

Leonidas Maroulis[1,2], Nikos Poulakakis[1,2], Konstantinos Proios[3], Danae Karakasi[2], Kostas A. Triantis[3], Moisis Mylonas[1,2], Katerina Vardinoyannis[2]

1 *Biology Department, School of Sciences and Engineering, University of Crete, Voutes University Campus, 70013 Irakleio, Greece*
2 *Natural History Museum of Crete, School of Sciences and Engineering, University of Crete, 71409 Irakleio, Greece*
3 *Faculty of Biology, Department of Ecology and Systematics, National and Kapodistrian University of Athens, Panepistimioupolis, 15784 Athens, Greece*

Corresponding author: Leonidas Maroulis (leomaroulis@gmail.com)

Abstract

Land snails and the Aegean Archipelago offer an intriguing combination for studying biodiversity, biogeography and ecology. A region with high environmental and temporal heterogeneity and a tri-continental biotic influence and a group of organisms with low active dispersal abilities, high endemism, as well as the particularity to leave shells as traces of past presence, set an ideal stage for testing biodiversity patterns and exploring multisource threats, especially in the era of the ongoing biodiversity crisis. In this study, we examine *Helix godetiana*, a large-sized, threatened and endemic land snail of the central and south Aegean Islands. The species has been extirpated from 22 of the 32 islands where it was historically present. We identify potential drivers of its extinction, as *Helix godetiana* faces several threats across its current range, including competitive exclusion by *Cornu aspersum*, a species with continuing expansion in the Aegean and climate change disrupting its unusual breeding cycle, which occurs in late spring. Our findings shed light on potentially major, yet previously unexplored, threats on endemic molluscs of the Aegean Islands, a European biodiversity hotspot.

Key words: Aegean Archipelago, biodiversity, extinction risks, islands, molluscs

OPEN ACCESS

Academic editor: Klaus Groh
Received: 4 June 2024
Accepted: 29 November 2024
Published: 16 January 2025

ZooBank: https://zoobank.org/49FA58CF-28E4-4E0C-B436-F542B2C0802E

Citation: Maroulis L, Poulakakis N, Proios K, Karakasi D, Triantis KA, Mylonas M, Vardinoyannis K (2025) On the path to extinction: *Helix godetiana* Kobelt, 1878, the only threatened *Helix* species in Greece. Nature Conservation 58: 1–10. https://doi.org/10.3897/natureconservation.58.129016

Copyright: © Leonidas Maroulis et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Islands contain a disproportionately high percentage of the world's biodiversity relative to their size, yet they also serve as hotspots for past, present and predicted future biodiversity loss (Russell and Kueffer 2019; Fernández-Palacios et al. 2021). Threatened species on islands usually have to face multiple threats simultaneously with biological invasions, wildlife exploitation and cultivation responsible for most insular extinctions (Leclerc et al. 2018). Moreover, over 60% of recorded terrestrial species extinctions since 1500 AD have been island endemics (Whittaker et al. 2017; Matthews and Triantis 2021).

Land snails are amongst the most studied and well-known invertebrate taxa on islands (Cameron et al. 2013), characterised by high species richness and notable rates of endemism (Proios et al. 2021). They are also one of the most threatened groups of terrestrial animals (Lydeard et al. 2004; Cowie et al. 2017),

comprising the majority of currently-known extinctions amongst all terrestrial plant and animal taxa (191 species out of 984, IUCN 2022), with over 70% occurring on islands (Régnier et al. 2009). Significant factors contributing to land snail extinctions include habitat loss, degradation and fragmentation, climate change, pollution and the introduction of invasive species (e.g. snails, rats, flatworms) (Holland 2009; Chiba and Cowie 2016). Particularly for European land snail species, the most significant threats are natural ecosystem modifications, residential and commercial development and agriculture (Neubert et al. 2019).

Obtaining detailed and accurate population data for snails, especially on remote islands, presents significant challenges. Consequently, distributional data serve as a major — and arguably the most useful — tool for assessing threat status and inferring extinction risk under the provisions of the IUCN Red List (see Criterion B, IUCN 2012). The 495 Aegean land snail species offer an exemplary case of particularly well-detailed knowledge of their island-specific distribution (Mylonas and Vardinoyannis 2022). Furthermore, land snails are amongst the most amenable invertebrates in this context, as their presence can be traced back in space and time due to their shell remains, thus providing a largely complete documentation of past extinction events (Cameron and Pokryszko 2005).

Given that biodiversity hotspots, areas of endemism and species with restricted distributions are pivotal concepts in biodiversity studies (Reid 1998), a deeper understanding of the mechanisms and processes driving the endangerment of land snails across the Aegean islands — a European biodiversity hotspot — is essential. Such insights could greatly enhance efforts to address the current extinction crisis, not only for snails, but for global biodiversity overall (Cowie et al. 2022).

In this study, we focus on a large-sized endemic species of the central and south-eastern Aegean, *Helix godetiana* Kobelt, 1878 (Fig. 1), which has been assessed as Endangered (EN) (IUCN 2022). This species is primarily found in maquis shrublands with a calcareous substrate and exhibits relatively small population sizes (Mylonas 1985). Numerous studies have attempted to clarify the phylogenetic position of *H. godetiana* and recent analyses, based on mitochondrial and nuclear markers, place it within the genus *Helix* as a distinct, monotypic subgenus (Korábek et al. 2021; Korábek and Hausdorf 2023). Based on extensive field data collected over the last 45 years and additional historical records, we document the past and present distribution of the species and explore the potential drivers of its decline.

Materials and methods

We compiled historical data on the distribution of *H. godetiana*, based on the existing extensive literature regarding Aegean islands' malacofauna (Fuchs and Käufel 1936; Mylonas 1982, 1985; Vardinoyannis 1994; Frank 1997; Triantis et al. 2008; Neubert 2014; Mylonas and Vardinoyannis 2022). We also reviewed the rich material held at the Natural History Museum of Crete (**NHMC**), collected over the past 45 years during numerous field trips organised to study the malacofauna of the Aegean Islands. Using this holistic approach, we provide an updated compilation of data on the distribution of *H. godetiana*.

We characterised the population as extant when museum material or bibliographic data confirmed the presence of living specimens or fresh shells.

Figure 1. *Helix godetiana* from Naxos Island.

Conversely, populations were considered extinct if only very old, subfossil shells were recorded (following Moody 1986).

It has been proposed that the relatively recent expansion of the more euryoecious Helicid species *Cornu aspersum*, *Cantareus apertus* and *Eobania vermiculata* may have acted as a restrictive factor for *H. godetiana* (Mylonas 1985). To examine the potential competitive effect of these three large helicid species and to determine whether the other indigenous *Helix* species of the region have similar effects, we employed a co-occurrence approach, testing the co-occurrence between extant *H. godetiana* and several Helicidae with presumably similar preferred habitats (i.e. *C. aspersum*, *C. aperta*, *E. vermiculata*, *H. nucula*, *H. figulina* and *H. cincta*). Using the material housed in the NHMC, we analysed all sampling localities (n = 766 from 40 islands) within the distributional range of *H. godetiana* (Fig. 2) where at least one of the above species was sampled extant, excluding subfossil and fossil shells. To quantify species co-occurrence, we applied the probabilistic model proposed by Veech (2013), which quantifies co-occurrence in a simple and straightforward way by counting the number of sampling sites where two species are found together. Observed co-occurrence is compared to expected co-occurrence, which is calculated as the product of the probabilities of occurrence for the two species multiplied by the number of sampling sites. The model uses combinatorics to assess whether the observed frequency of co-occurrence is significantly higher than expected (indicating a positive association), significantly lower than

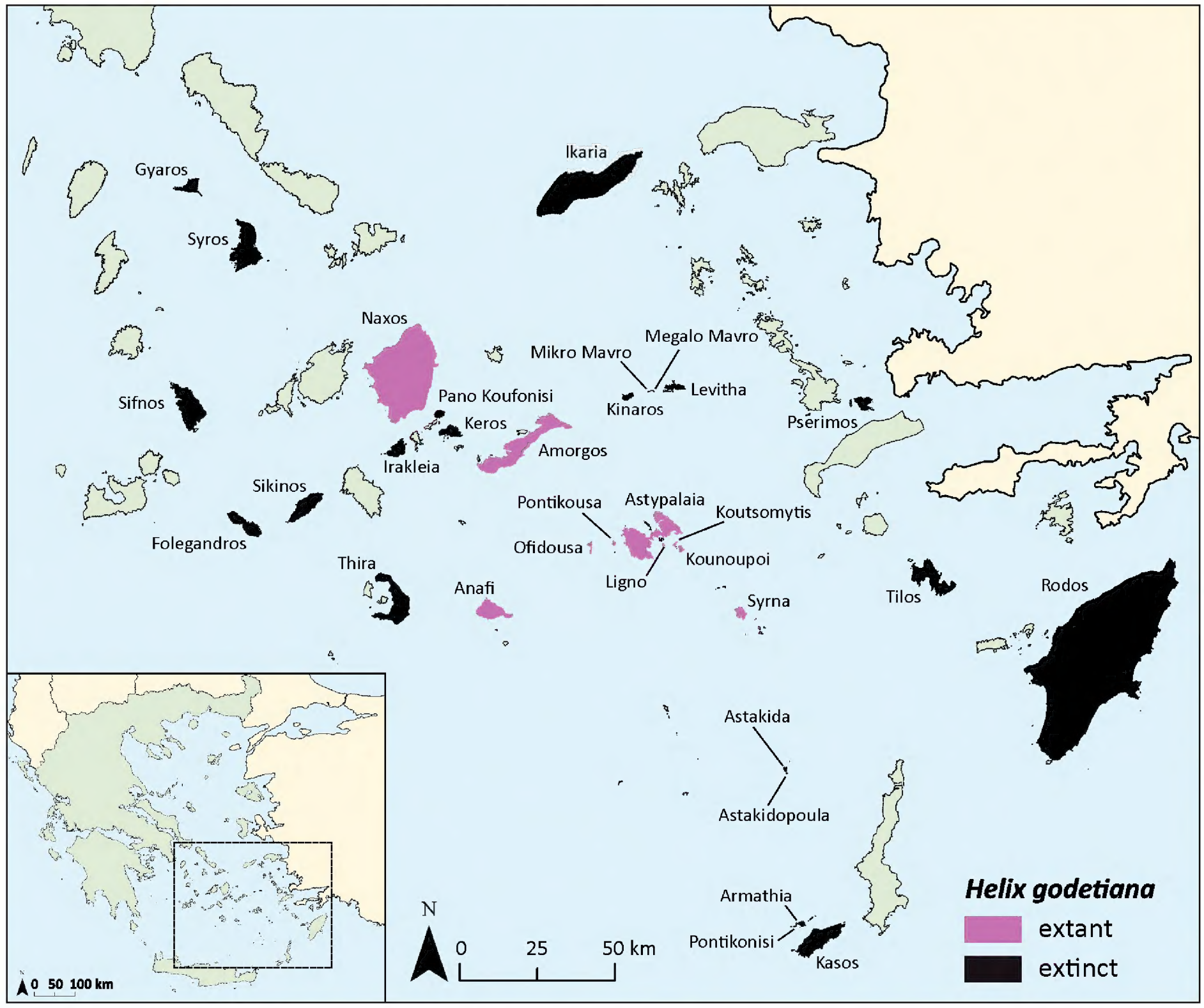

Figure 2. The distribution of *H. godetiana*. Pink shows where the species is currently extant, while black depicts the islands where only old shells are encountered.

expected (indicating a negative association) or not significantly different from expected (indicating a random association) (Veech 2013; Griffith et al. 2016). In cases where negative correlation was found (i.e. $P_{lt} < 0.05$), we considered that the species is highly likely to be negatively influenced by the presence of another species (but see also Blanchet et al. 2020). The analysis was conducted in R (R Core Team 2024) using the package "cooccur" (Griffith et al. 2016).

Results

Herein, we present an updated profile of the past and present distribution of *H. godetiana* (Fig. 2), which has historically inhabited 32 islands, but is currently found extant on only 10. This represents a reduction to 31% of its original distribution (Table 1, Fig. 2)

Additionally, we present the species co-occurrence probabilities with other helicid snails, using it as a proxy to assess potential competitive interactions. We note its negative association with *C. aspersum*, with which *H. godetiana* does not co-exist in any locality (Table 2). Apart from *C. aspersum*, its association with every other helicid species is not different from the null expectations.

Table 1. Aegean Islands where *H. godetiana* is distributed. EX indicates that only fossil or subfossil shells have been found and that the snail is probably locally extinct. Bold indicates a new record of this species for the island, based on the material examined from NHMC specimens. B indicates only a bibliographic record.

Island / Species	*H. godetiana*
Amorgos	+
Anafi	+
Armathia islet (Kasos)	**EX**
Astakida islet (Syrna)	EX
Astakidopoula islet (Syrna)	EX
Astypalaia	+
Folegandros	EX
Gyaros	**EX**
Ikaria	**EX**
Irakleia	EX
Kasos	EX
Keros	EX
Kinaros islet (between Amorgos – Patmos)	**EX**
Koutsomytis islet (Astypalaia)	+
Kounoupoi islet (Astypalaia)	+
Levitha (between Amorgos – Patmos)	**EX**
Ligno islet (Astypalaia)	+
Megalo Mavro islet (between Amorgos – Patmos)	**EX**
Mikro Mavro islet (between Amorgos – Patmos)	**EX**
Naxos	+
Ofidousa islet (Astypalaia)	+
Pano Koufonisi	EX
Pontikousa islet (Astypalaia)	+
Pontikonisi islet (Kasos)	**EX**
Pserimos	**EX**
Sifnos	EX
Sikinos	EX
Syros	EX
Syrna	+
Rodos	EX (B)
Thira	EX
Tilos	EX

Discussion

Overall, our study demonstrates a notable decrease in the distribution and population size of *H. godetiana*, one of the largest endemic snails of the Aegean. Based on extensive field data spanning more than four decades, *H. godetiana* has become extinct on the majority of the islands where it was once found and is now restricted to the central islands of its former range (Fig. 2). Moreover, recent comprehensive sampling expeditions to Naxos, Anafi, Astypalaia and Syrna islands yielded only sparse shells in sites where the species was previously abundant, suggesting declining populations on islands where the species is still extant and indicating that the species is on the path to extinction.

Table 2. Co-occurrence analysis on the pairwise species associations of *Helix godetiana* with the three non-native large helicids (*C. apertus*, *C. aspersum* and *E. vermiculata*) and three native *Helix* species across the distributional range of *H. godetiana* in the Aegean Archipelago. sp1_inc: number of localities where *H. godetiana* was found as extant, sp2_inc: number of localities in the Aegean Islands across where the respectively compared species are present (based on data from the NHMC), obs_cooc: observed number of sites with both species, exp_cooc: expected number of sites with both species, p_lt: probability of co-occurrence of the species pair at a frequency smaller than the observed frequency, p_gt: probability of co-occurrence of the species pair at a frequency greater than the observed frequency. Bold indicates statistically significant probability ($P < 0.05$).

Species 1	Species 2	sp1_inc	sp2_inc	obs_cooc	exp_cooc	p_lt	p_gt
H. godetiana	*C. apertus*	24	157	6	4.9	0.80	0.37
H. godetiana	*C. aspersum*	24	221	0	6.9	**0.0002**	1
H. godetiana	*E. vermiculata*	24	600	20	18.8	0.80	0.38
H. godetiana	*H. cincta*	24	57	1	1.8	0.45	0.85
H. godetiana	*H. figulina*	24	142	3	4.4	0.32	0.85
H. godetiana	*H. nucula*	24	125	1	3.9	0.08	0.99

Undoubtedly, contemporary threats such as intensive grazing, fire and habitat destruction and degradation, continue to pose significant risks to invertebrate species, with these impacts likely amplified for large, slow-moving organisms like helicid snails. Could these factors, coupled with the species' intrinsic traits, such as large body size, be responsible for the observed range contractions? Large body size has been correlated with several extinction-promoting traits (McKinney 1997; Purvis et al. 2000) and is linked to higher extinction risk across various animal taxa (Chiba and Roy 2011; Seibold et al. 2015; Terzopoulou et al. 2015; Verde Arregoitia 2016). However, considering that *H. godetiana* is the only threatened species within the iconic, large-sized genus *Helix* in Greece, the reasons for its predicament likely extend beyond just shell size. Several synergistic factors appear to be driving the species toward extinction.

Firstly, a potentially major drawback of *H. godetiana* is its reproductive behaviour, as it has been observed to copulate and lay eggs at the end of spring, specifically in May on Naxos Island (Mylonas, personal observation). With late spring temperatures rising and precipitation decreasing on several Aegean Islands, shifting them towards semi-arid conditions (Myronidis and Nikolaos 2021), hatchlings must endure the hot and dry summer months, aestivating in the soil and ground, thereby facing increased risks of desiccation and predation. This reproductive strategy deviates strikingly from that of most land snails in the Aegean, as nearly all species copulate and lay eggs after the first autumnal rains or rarely in early spring (Vardinoyannis et al. 2018). There is a considerable possibility that the reproductive strategy of *H. godetiana* was well-adapted to the climatic conditions of several millennia ago, when the area was less arid and had higher levels of precipitation. However, this strategy may no longer be viable due to modern climate change, making *H. godetiana* one of the first documented land snail species severely threatened by climate change. Interestingly, species of the genus *Codringtonia* in the Peloponnese, which exhibit a similar — peculiar and rare in the area — breeding cycle, also show declining populations, as reported by Hadjicharalambous (1996).

Secondly, based on co-occurrence probabilities, we tested whether the expansion of the large non-native snails *Cantareus apertus*, *Cornu aspersum* and *Eobania vermiculata* across several Aegean Islands had a possible influence on the diminishing distribution of *H. godetiana*. This hypothesis is partially supported, as only *C. aspersum* has a negative and statistically significant association with *H. godetiana* (Table 2). On the other hand, sympatric occurrences of *E. vermiculata* and *C. apertus* with *H. godetiana* do not differ from random expectations (Table 2), despite their relatively close preferred habitats and perceived ecological niches. Therefore, *C. aspersum* is a possible restricting factor for the survival of *H. godetiana*.

Finally, *H. godetiana* is an edible snail and human exploitation as a food source (Mylonas and Vardinoyannis 2022) has likely contributed to its decreased occurrence across Aegean Islands. While not the primary driver of its decline, this factor could compound the effects of other threats, further exacerbating the species' vulnerability.

Molluscs, constituting the second-largest animal phylum, are a reasonably well-known group of invertebrates and identifying the reasons for the decline of particular species holds strong potential for altering the Earth's trajectory towards a Sixth Mass Extinction (Cowie et al. 2022). *Helix godetiana* presents a characteristic case study as an endemic island snail facing cascading effects from competition with a non-indigenous (yet well-established and expanding) snail (*C. aspersum*), climate change disrupting its breeding cycle and human exploitation as a food source, coupled with habitat degradation and land use changes on islands that pose a significant threat to numerous species.

Acknowledgements

We would like to thank Ruud Bank and Bernhard Hausdorf for their valuable comments on a previous version of the manuscript, which have notably improved this paper.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was partially funded by the General Secretariat for Research and Technology (GSRT) and the Hellenic Foundation for Research and Innovation (HFRI), under the HFRI Support of Faculty Members (DEP) and Researchers (GA. number HFRI-FM17-488).

Author contributions

Conceptualization: KV, LM, KAT, MM. Data curation: KV. Formal analysis: LM. Investigation: MM, KV, LM. Methodology: KAT, LM, KV, MM. Project administration: KV. Supervision: NP. Validation: KP. Visualization: DK. Writing - original draft: LM. Writing - review and editing: KAT, KV, MM, NP, LM, DK, KP.

Author ORCIDs

Leonidas Maroulis https://orcid.org/0000-0002-9399-8417
Nikos Poulakakis https://orcid.org/0000-0002-9982-7416
Konstantinos Proios https://orcid.org/0000-0001-7545-5892
Danae Karakasi https://orcid.org/0009-0001-5397-8876
Kostas A. Triantis https://orcid.org/0000-0003-2737-8890
Katerina Vardinoyannis https://orcid.org/0000-0001-7368-0965

Data availability

All of the data that support the findings of this study are available in the main text.

References

Blanchet FG, Cazelles K, Gravel D (2020) Co-occurrence is not evidence of ecological interactions. Ecology Letters 23(7): 1050–1063. https://doi.org/10.1111/ele.13525

Cameron RAD, Pokryszko B (2005) Estimating the species richness and composition of land mollusc communities: Problems, consequences and practical advice. Journal of Conchology 38(5): 529–548. https://doi.org/10.5962/p.408170

Cameron RAD, Triantis KA, Parent CE, Guilhaumon F, Alonso MR, Ibáñez M, de Frias Martins AM, Ladle RJ, Whittaker RJ (2013) Snails on oceanic islands: Testing the general dynamic model of oceanic island biogeography using linear mixed effect models. Journal of Biogeography 40(1): 117–130. https://doi.org/10.1111/j.1365-2699.2012.02781.x

Chiba S, Cowie RH (2016) Evolution and Extinction of Land Snails on Oceanic Islands. Annual Review of Ecology, Evolution, and Systematics 47(1): 123–141. https://doi.org/10.1146/annurev-ecolsys-112414-054331

Chiba S, Roy K (2011) Selectivity of terrestrial gastropod extinctions on an oceanic archipelago and insights into the anthropogenic extinction process. Proceedings of the National Academy of Sciences of the United States of America 108(23): 9496–9501. https://doi.org/10.1073/pnas.1100085108

Cowie RH, Régnier C, Fontaine B, Bouchet P (2017) Measuring the sixth extinction: What do mollusks tell us? The Nautilus 131: 3–41.

Cowie RH, Bouchet P, Fontaine B (2022) The sixth mass extinction: Fact, fiction or speculation? Biological Reviews of the Cambridge Philosophical Society 97(2): 640–663. https://doi.org/10.1111/brv.12816

Fernández-Palacios JM, Kreft H, Irl SDH, Norder S, Ah-Peng C, Borges PAV, Burns KC, de Nascimiento L, Meyer J-Y, Montes E, Drake DR (2021) Scientists' warning—The outstanding biodiversity of islands is in peril. Global Ecology and Conservation 31: e01847. https://doi.org/10.1016/j.gecco.2021.e01847

Frank C (1997) Die Molluskenfauna der Insel Rhodos, 2. Teil. Stapfia 48: 1–179.

Fuchs A, Käufel F (1936) Anatomische und systematische Untersuchungen an Land- und Süßwasser- schnecken aus Griechenland und von den Inseln des Ägäischen Meeres. Archiv für Naturgeschichte, Zeitschrift für systematische zoologie 5: 541–662.

Griffith DM, Veech JA, Marsh CJ (2016) cooccur: Probabilistic Species Co-Occurrence Analysis in R. Journal of Statistical Software 69(Code Snippet 2): 1–17. https://doi.org/10.18637/jss.v069.c02

Hadjicharalambous E (1996) Contribution to the study of the ecology and biology of the genus *Codringtonia* Kobelt, 1898 (Gastropoda, Pulmonata). PhD Thesis, University of Athens, Athens.

Holland B (2009) Land snails. In: Gillespie R, Clauge D (Eds) Encyclopedia of Islands. University of California Press, Oakland, 537–542. https://doi.org/10.1525/9780520943728-125

IUCN (2012) IUCN Red List Categories and Criteria: Version 3.1. 2nd edn. IUCN, Gland, Switzerland and Cambridge, UK, [iv +] 32 pp.

IUCN (2022) IUCN. https://www.iucnredlist.org/ [Accessed: 2022-6-20]

Korábek O, Hausdorf B (2023) Unravelling the double *Helix escherichi*, with description of *Helix ankae* sp. nov. and a discussion of *Maltzanella* and the subgenera of *Helix* (Gastropoda: Helicidae). Archiv für Molluskenkunde 152(2): 239–256. https://doi.org/10.1127/arch.moll/152/239-256

Korábek O, Juřičková L, Petrusek A (2021) Diversity of land snail tribe Helicini (Gastropoda: Stylommatophora: Helicidae): Where do we stand after 20 years of sequencing mitochondrial markers? Diversity 14(1): 24. https://doi.org/10.3390/d14010024

Leclerc C, Courchamp F, Bellard C (2018) Insular threat associations within taxa worldwide. Scientific Reports 8(1): 6393. https://doi.org/10.1038/s41598-018-24733-0

Lydeard C, Cowie RH, Ponder WF, Bogan AE, Bouchet P, Clark SA, Cummings KS, Frest TF, Gargominy O, Herbert DG, Hershler R, Perez KE, Roth B, Seddon M, Strong EE, Thompson FG (2004) The global decline of nonmarine mollusks. Bioscience 54(4): 321–330. https://doi.org/10.1641/0006-3568(2004)054[0321:TGDONM]2.0.CO;2

Matthews TJ, Triantis KA (2021) Island biogeography. Current Biology 31(19): R1201–R1207. https://doi.org/10.1016/j.cub.2021.07.033

McKinney ML (1997) Extinction vulnerability and selectivity: Combining ecological and paleontological views. Annual Review of Ecology and Systematics 28(1): 495–516. https://doi.org/10.1146/annurev.ecolsys.28.1.495

Moody R (1986) FOSSILS. How to find and identify over 300 genera. Hamlyn Publishing Group, England, 192 pp.

Mylonas M (1982) The zoogeography and ecology of the terrestrial molluscs of Cyclades. PhD Thesis, University of Athens, Athens.

Mylonas M (1985) The distribution and ecology of the species *Helix godetiana* Kobelt (Gastropoda: Pulmonata). Biologia Gallo-Hellenica 10: 139–142.

Mylonas M, Vardinoyannis K (2022) The terrestrial malacofauna of the Southeast – Central Aegean islets. Journal of Conchology 44(4): 317–334.

Myronidis D, Nikolaos T (2021) Changes in climatic patterns and tourism and their concomitant effect on drinking water transfers into the region of South Aegean, Greece. Stochastic Environmental Research and Risk Assessment 35(9): 1725–1739. https://doi.org/10.1007/s00477-021-02015-y

Neubert E (2014) Revision of *Helix* Linnaeus, 1758 in its eastern Mediterranean distribution area, and reassignment of *Helix godetiana* Kobelt, 1878 to *Maltzanella* Hesse, 1917 (Gastropoda, Pulmonata, Helicidae). Contributions to Natural History 26: 1–200.

Neubert E, Seddon MB, Allen DJ, Arrébola J, Backeljau T, Balashov I, Bank R, Cameron RAD, de Frias Martins AM, De Mattia W, Dedov I, Duda M, Falkner G, Falkner M, Fehér Z, Gargominy O, Georgiev D, Giusti F, Gómez Moliner BJ, Groh K, Ibáñez M, Kappes H, Manganelli G, et al. (2019) European Red List of terrestrial molluscs. IUCN, Cambridge, UK and Brussels, Belgium. https://portals.iucn.org/library/node/48439

Proios K, Cameron RAD, Triantis KA (2021) Land snails on islands: Building a global inventory. Frontiers of Biogeography 13(2): e51126. https://doi.org/10.21425/F5FBG51126

Purvis A, Gittleman JL, Cowlishaw G, Mace GM (2000) Predicting extinction risk in declining species. Proceedings. Biological Sciences 267(1456): 1947–1952. https://doi.org/10.1098/rspb.2000.1234

R Core Team (2024) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Régnier C, Fontaine B, Bouchet P (2009) Not knowing, not recording, not listing: Numerous unnoticed mollusk extinctions. Conservation Biology 23(5): 1214–1221. https://doi.org/10.1111/j.1523-1739.2009.01245.x

Reid WV (1998) Biodiversity hotspots. Trends in Ecology & Evolution 13(7): 275–280. https://doi.org/10.1016/S0169-5347(98)01363-9

Russell J, Kueffer C (2019) Island Biodiversity in the Anthropocene. Annual Review of Environment and Resources 44(1): 31–60. https://doi.org/10.1146/annurev-environ-101718-033245

Seibold S, Brandl R, Buse J, Hothorn T, Schmidl J, Thorn S, Müller J (2015) Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. Conservation Biology 29(2): 382–390. https://doi.org/10.1111/cobi.12427

Terzopoulou S, Rigal F, Whittaker RJ, Borges PAV, Triantis KA (2015) Drivers of extinction: The case of Azorean beetles. Biology Letters 11(6): 20150273. https://doi.org/10.1098/rsbl.2015.0273

Triantis KA, Vardinoyannis K, Mylonas M (2008) Biogeography, land snails and incomplete data sets: The case of three island groups in the Aegean Sea. Journal of Natural History 42(5–8): 467–490. https://doi.org/10.1080/00222930701835431

Vardinoyannis K (1994) Biogeography of land snails in the south Aegean island Arc. PhD Thesis, University of Athens, Athens.

Vardinoyannis K, Parmakelis A, Triantis KA, Giokas S (2018) Land molluscs in Greece: The rich, unique, diverse and unprotected animal models. In: Sfenthourakis S, Pafilis P, Parmakelis A, Poulakakis N, Triantis K (Eds) Biogeography and biodiversity of the Aegean. In honour of Prof. Moysis Mylonas. Broken Hill Publishers Ltd, Nicosia, 47–66.

Veech JA (2013) A probabilistic model for analysing species co-occurrence. Global Ecology and Biogeography 22(2): 252–260. https://doi.org/10.1111/j.1466-8238.2012.00789.x

Verde Arregoitia LD (2016) Biases, gaps, and opportunities in mammalian extinction risk research. Mammal Review 46(1): 17–29. https://doi.org/10.1111/mam.12049

Whittaker RJ, Fernández-Palacios JM, Matthews TJ, Borregaard MK, Triantis KA (2017) Island biogeography: Taking the long view of nature's laboratories. Science 357(6354): eaam8326. https://doi.org/10.1126/science.aam8326